EFFECTS OF NITROGEN AND PHOSPHORUS ADDITION ON SOIL RESPIRATION IN NORTHERN HARDWOOD FORESTS

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ABSTRACT

Soil respiration - the CO_2 efflux from the forest soil surface - is an important indicator of root and microbial activity and is sensitive to global changes such as climate warming, anthropogenic nitrogen deposition and elevated atmospheric CO_2. I evaluated the response of total soil respiration (TSR) to changes in soil nutrient availability in temperate deciduous forests in New Hampshire. Low-level N (3 g/m^2/year), P (1 g/m^2/year) or N + P have been applied annually to thirteen northern hardwood stands of different age and site quality since 2011. My analysis of TSR for 2013, 2014, 2016, and 2017 confirmed the overall suppression effect of N addition across these stands ($p < 0.001$), but the responses varied considerably among stands. No consistent effects of P addition on TSR were detected, but a significant interaction between N and P and forest age was observed ($P = 0.04$). No correlation was detected between the TSR response ratio ((treatment-control)/control) and either pre-treatment soil fertility indexes, or the response ratio of soil microbial respiration measured in the laboratory. Overall, the significant interaction of N and P and forest age suggests that the responses of TSR rates in northern hardwood forests depend on forest age as well as the nutrients applied (N, P, or N+P). Perhaps the variation in the response of TSR to nutrient additions among the stands might be attributed in part to differences in root respiration.

BIOGRAPHICAL SKETCH

Shiyi Li obtained her B.A. in English Language and Literature from Shanghai International Studies University and a Master of Public Administration at Cornell. Always curious and passionate about the natural world, she is now on her new journey to study various intriguing ecological processes in the forests.

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TABLE OF CONTENTS

1. Introduction

Soil respiration is one of the most important flux pathways in the global C cycle, ranking as the third largest pathway behind ocean uptake and terrestrial plant photosynthesis (ca. 75 Pg C/year; Schlesinger and Andrews, 2000). It is an important indicator of below-ground carbon cycling (Janssens et al., 2010) as well as other nutrient cycles. By definition, total soil respiration (TSR) is the CO_2 released from the soil surface, and it consists of autotrophic respiration (includes respiration by root tissues, mycorrhizal fungi, and other rhizosphere organisms) and heterotrophic respiration (mostly by microbial decomposers, bacteria and saprotrophic fungi). In forest ecosystems both of these components make a substantial contribution to TSR, but empirical separation of autotrophic and heterotrophic soil respiration in the field is notoriously difficult (Bond-Lamberty et al., 2004). Current estimates suggest that roughly similar proportions are contributed by the two components in temperate forest ecosystems, but considerable variation among sites has been reported (Hanson et al., 2000).

The amount of TSR that occurs in an ecosystem is driven by multiple factors that affect autotrophic and heterotrophic respiration. Temperature is directly linked to metabolic rates of both root cells (Atkin et al., 2000) and microorganisms (Mikan et al., 2002); an increase of soil temperature causes higher TSR rates until a point where high temperatures result in dysfunction of soil microorganisms. Soil moisture also influences TSR, but only the highest and lowest soil moisture levels are likely to limit TSR in most ecosystems (Xu et al., 2004).

TSR is also sensitive to chronic nitrogen deposition and nitrogen fertilization. A meta-analysis reported that low-level nitrogen additions (<5 g/m^2/year) often but not always result in a decrease in TSR rates (Janssens et al., 2010). The reasons for variability in response are complex and not fully understood. Suppression of microbial respiration and litter decomposition rates by added N has been observed in many studies, and has been linked in part to decreased activity of lignin-degrading enzymes (Saiya-Cork et al., 2002). Nitrogen addition could also reduce autotrophic respiration if relief of N limitation results in a decrease in belowground C allocation. Indeed, Bae et al. (2015) observed that total belowground C allocation decreased with increasing N availability across a soil fertility gradient in northern hardwood forests. In addition, in theory another limiting nutrient like phosphorus (Vadeboncoeur, 2010; Goswami et al., 2018) could change TSR through alteration of microbial activity or the production and maintenance of fine root biomass. For example, there is evidence that microbial respiration can be stimulated by P addition (Fisk et al., 2014). However, Kang et al. (2016) did not observe clear effects of short-term P addition on TSR in northern hardwood forest ecosystems.

Another factor that could affect the response of TSR to nutrient additions is forest age. According to the forest co-limitation model of Rastetter et al. (2013), successional northern hardwood forests that were recently harvested should be more limited by N while P limitation or NP co-limitation should gradually develop as the forests mature. In fact, recent observations of Goswami et al. (2018) indicated that aboveground

production of young northern hardwood stands in NH were mostly N limited whereas mid-age and mature forests were mostly P limited, perhaps reflecting in part long-term anthropogenic N pollution in this region and consequent transactional P limitation (Vitousek et al., 2010). The implications of this observation for belowground C allocation and TSR are unknown.

To further examine the effects of nutrient addition on TSR in northern hardwood forests, I analyzed four years of TSR data (2013, 2014, 2016, 2017) collected from the same forest stands studied by Bae et al. (2015), Kang et al. (2016) and Goswami et al. (2018). These forests have received annual fertilization with N and P in a full factorial design since 2011. The complex effects of NP co-limitation on forest ecosystem processes have received limited study, and I hoped to resolve some of the factors contributing to variation in C cycling responses to changes in soil nutrient availability. I hypothesized that the response of TSR to nutrient additions would differ between young and older northern hardwood stands. In young, N-limited stands N addition should result in decreased TSR because of N suppression of microbial activity and possibly also decreased plant C allocation to roots. In contrast, in older, P-limited stands I expected the greatest decline in TSR in N+P treated plots, again reflecting N suppression of microbial heterotrophs and reduced C allocation to roots when P limitation is relieved. I hoped that this study of NP co-limitation of TSR would contribute to a better understanding of the intricate mechanisms whereby anthropogenic N addition could be altering the biogeochemical dynamics of temperate

forests and thereby contributing to changes in the global carbon cycle (Wieder et al., 2014).

2. Methods

2.1 Study Site

This ongoing forest fertilization experiment is conducted at three sites in the White Mountain National Forest, NH, USA: Bartlett Experimental Forest (BEF: 44° 02–04' N, 71° 16–19' W; elevation 330–570 m), Hubbard Brook Experimental Forest (HBEF: 43° 56' N, 71° 44' W; elevation 500 m), and Jeffers Brook (JB: 44° 02' N, 71° 53' W; elevation 730 m) (Figure 1). The study area has temperate, humid continental climate with July and January temperatures of 19 and -9 ℃, respectively at 450 m elevation. The precipitation is evenly distributed throughout the year and varies only slightly across the study sites, with annual values ranging from 1270 to 1400 mm (Bae et al., 2015; Kang et al., 2016). The soils from the three sites are mostly glacial till-derived Spodosols (Typic Haplorthods), with granite and gneiss parent materials predominating at BEF, quartz monzonite and mica schist at HBEF, and amphibolite at JB. These differences lead to variation in inherent soil fertility among the three sites: BEF has the lowest and JB the highest N mineralization and Ca availability (Bae et al., 2015) (Table 1).

All thirteen forest stands covered in this study have been harvested in the past and they are categorized into three age classes in terms of the stage of succession: young (<30 years; three at BEF), mid-age (40-50 years; three at BEF, one each at JB and HBEF), and old (>80 years; three at BEF, one each at JB and HBEF). The old stands are dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula allegheniensis* Britt.). Younger stands are

also dominated by a variable mixture of maple-beech-yellow birch, plus early successional species, paper birch (*Betula papyrifera* Marsh.), pin cherry (*Prunus pennsylvanica* L.f.), red maple (*Acer rubrum* L.) and aspen (*Populus grandidentata* Michaux.).

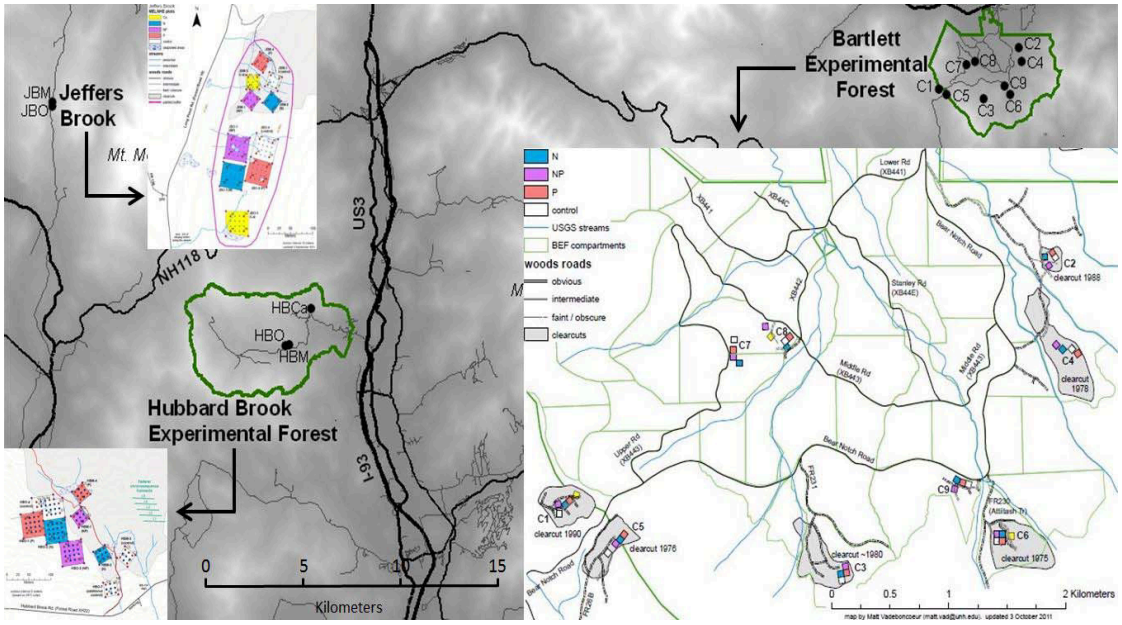

Figure 1. Map of the study sites

Stand	Forest age	Year cut	Elevation (m)	Soil N mineralization (μg g^{-1} soil d^{-1})	Litterfall N flux (g N m^{-2} $year^{-1}$)	Basal area (m^2 ha^{-1})	Dominant species
Bartlett, C1	Young	1990	570	0.3	2.82	25.2	*Betula papyrifera, Prunus pensylvanica, Fagus grandifolia*
Bartlett, C2	Young	1988	340	0.31	2.35	23.4	*Acer rubrum, F. grandifolia, B. papyrifera*
Bartlett, C3	Young	1985	590	0.46	na	30.5	*P. pensylvanica, F. grandifolia, A. rubrum*
Bartlett, C4	Mid-age	1979	410	0.38	3.23	32.9	*B. papyrifera, Populus grandidentata, P. pensylvanica*

Bartlett, C5	Mid-age	1976	550	0.45	na	27.2	*B. papyrifera, P. pensylvanica, A. rubrum*
Bartlett, C6	Mid-age	1975	460	0.49	2.90	30.1	*A. rubrum, B. papyrifera, F. grandifolia*
Bartlett, C7	Old	1890	440	0.36	na	32.1	*F. grandifolia, A. saccharum, Tsuga canadensis*
Bartlett, C8	Old	1883	330	0.27	2.40	35.2	*F. grandifolia, A. saccharum, B. alleghaniensis*
Bartlett, C9	Old	1890	440	0.38	3.07	32.7	*A. saccharum, F. grandifolia, B. alleghaniensis*
Hubbard Brook Mid	Mid-age	1970	500	0.58	4.29	29.5	*B. alleghaniensis, B. papyrifera, A. rubrum*
Hubbard Brook Old	Old	1911-1913	500	0.71	3.60	33.9	*B. alleghaniensis, F. grandifolia, A. saccharum*
Jeffers Brook Mid	Mid-age	1974	730	0.59	2.84	27.9	*B. alleghaniensis, B. papyrifera, A. saccharum*
Jeffers Brook Old	Old	1915-1929	730	0.54	2.48	35.7	*A. saccharum, B. alleghaniensis, F. grandifolia*

Table 1. Site characteristics of thirteen northern hardwood forest stands in central New Hampshire, USA used in the present study

2.2 Experimental Design

Each forest stand has four 50 x 50 m experimental plots (30 x 30 m for mid-age stands at JB and HB). The four plots of each stand were established close to each other, and share similar topography, forest species composition, and soil types. Data are collected from the interior 30 x 30 m (20 x 20 m for mid-age stands at JB and HB) square of each treatment plot (i.e. 10 m wide treated buffer zone for each plot). The four plots in each stand were assigned randomly to the full 2 x 2 factorial treatments: control, N

addition, P addition, and N + P addition, but with control plots never located directly downslope of fertilized plots.

Fertilizers have been applied uniformly by hand to each plot beginning in 2011. Nitrogen plots were treated by NH_4NO_3, 3 g/m^2/year; phosphorus plots were treated by NaH_2PO_4, 1 g/m^2/year; N + P received both fertilizers; control plots were not treated by fertilizers but received trampling that is associated with fertilization treatment. The fertilizer additions are conducted in mid-May to early June each year.

2.3 TSR

Flux of CO_2 from the soil was measured each plot using a LI-8100 Fco_2 system (Licor Biosciences, Lincoln, NE). Five PVC collars (20 cm diameter) were approximately systematically-installed in each plot prior to measurements that began in May 2010, avoiding any big tree roots and boulders. In 2014, two more collars were added to each plot. Collars disturbed by animal activity were reinstalled at nearby locations prior to measurement, early in the field season each year. TSR was measured between 9 AM and 4 PM in each plot during the growing season, May - September. In 2013-2014, 2016-2017 about five measurements were made in all the plots except for 2017 when only two measurements were made. In 2017 JB stands were only measured once in late June due to road destruction in a rainstorm. In 2015 only three stands were measured and these data are excluded from this study.

2.4 Soil Temperature

Soil temperature at 5 or 10 cm depth was also measured nearby the soil respiration collar whenever TSR was measured. In 2013 and 2014, soil temperatures were measured at 5 cm below the surface whereas in 2016 and 2017 temperature was measured at 10 cm depth. To adjust these data to a common depth, I extracted data from the HBEF soil temperature monitoring site (Soil Climate Analysis Network; www.wcc.nrcs.usda.gov/nwcc/site?sitenum=2069&state=nh). and used the daytime (0900-1600) average difference between 5 cm and 10 cm for the date of each set of measurements to adjust soil temperature to the 10 cm depth at all thirteen stands.

2.5 Statistical Analysis

I tested treatment effects on TSR using a linear mixed-effects model (lme4 package, Bates et al., 2015) in R (R Core Team, 2016). I modeled treatment (N or P addition) and forest age as fixed effects, the random temporal effect of when the measurement was taken (early or late in a month) in a specific year, and the random spatial effect of where the collar was located (respiration collar nested in plot that nested in stand that nested in a forest site). I also included the categorical variable year as a blocking factor and the continuous variable soil temperature as a covariate. This factorial approach compares response variable in plots with N addition (i.e., N and N+P plots) to those with no N addition (i.e., control and P plots) and plots with P addition to those with no P addition, and also tests the interaction between N and P additions, as well as the interaction between treatment and forest age. In the end, I used post-hoc Tukey comparisons of least-squares means (lsmeans package, Lenth 2016) to test the

differences between treatments within age class. I considered P values < 0.05 to be significant but also report trends for which P values were between 0.05 - 0.10.

3. Results

The overall mixed model indicated a very strong effect of N addition on TSR (Table 2). However, the effects of fertilization treatments on TSR were not consistent across all stands (Table 2 and figure 2). In particular, stand age explained some of the variation in treatment response, as there was a statistically significant interaction of age x N x P ($p = 0.04$). In addition, the effect of adding N also depended on adding P or not, indicated by significant N x P interaction ($p = 0.04$). In the young stands, N treated plots had significantly lower TSR rates than the control plots ($p < 0.01$). However, adding P or N + P did not have obvious effects in young, mid-age or old stands (Figure 2). In summary, the overall highly significant N suppression effect was driven primarily by the strong response in young stands. In mid-age and old stands, treatment did not have significant effect on TSR.

As expected, there was a highly significant quadratic relationship between TSR and soil temperature ($p < 0.0001$). This covariate successfully reduced the unexplained variation in this model (Figure 3).

	Sum Sq	Mean Sq	NumDF	DenDF	F.value	Pr(>F)	
Nadd	1.1897	1.18966	1	30.8	13.975	0.0007582	***
Padd	0.0195	0.01949	1	30.1	0.229	0.6357902	
Age	0.9824	0.49118	2	9.5	5.770	0.0229775	*
Year	0.7585	0.25282	3	11.8	2.970	0.0753302	.
poly(SoilTemp, 2)	6.2948	3.14738	2	3726.3	36.972	< 2.2e-16	***
Nadd:Padd	0.3874	0.38737	1	30.8	4.550	0.0409956	*
Nadd:Age	0.1015	0.05075	2	30.7	0.596	0.5572070	
Padd:Age	0.1054	0.05272	2	30.0	0.619	0.5450755	
Nadd:Padd:Age	0.6224	0.31118	2	30.7	3.655	0.0376858	*

Table 2. Mixed-effects model of TSR during the growing seasons of 2013 – 2014 and 2016 – 2017 in treated (N, P and N + P) and control plots of thirteen forest stands of three ages (young, mid-age and old).

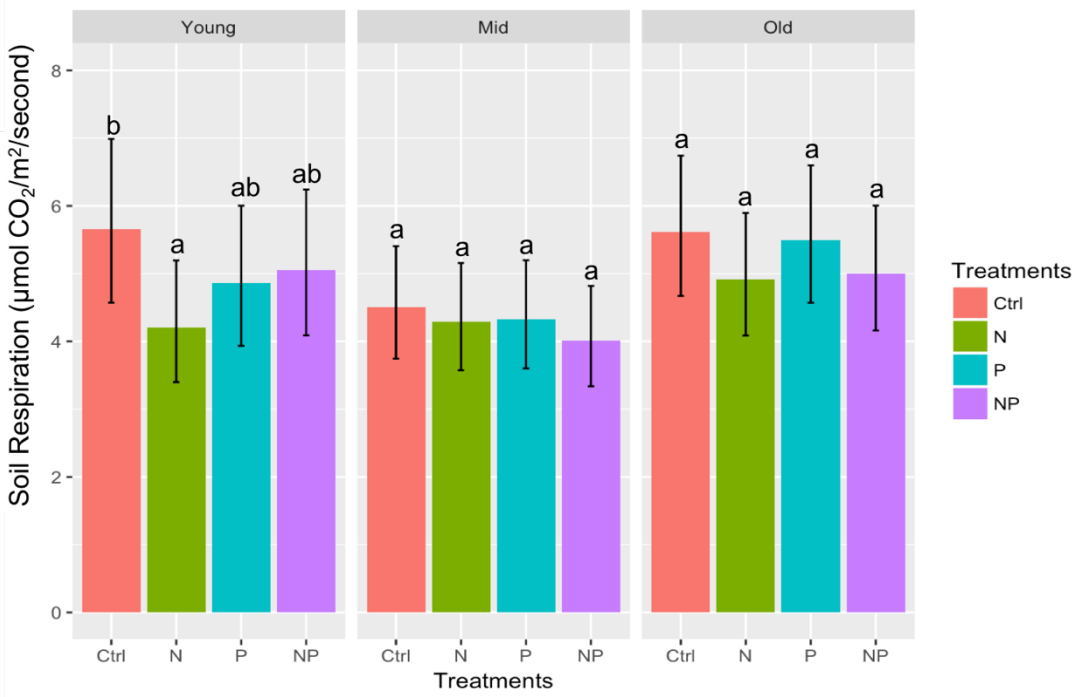

Figure 2. The mean soil respiration rates (+/- SE) over four years of measurement (2013, 2014, 2016, 2017) by age and treatment; bars with different letters are significantly different ($p < 0.05$).

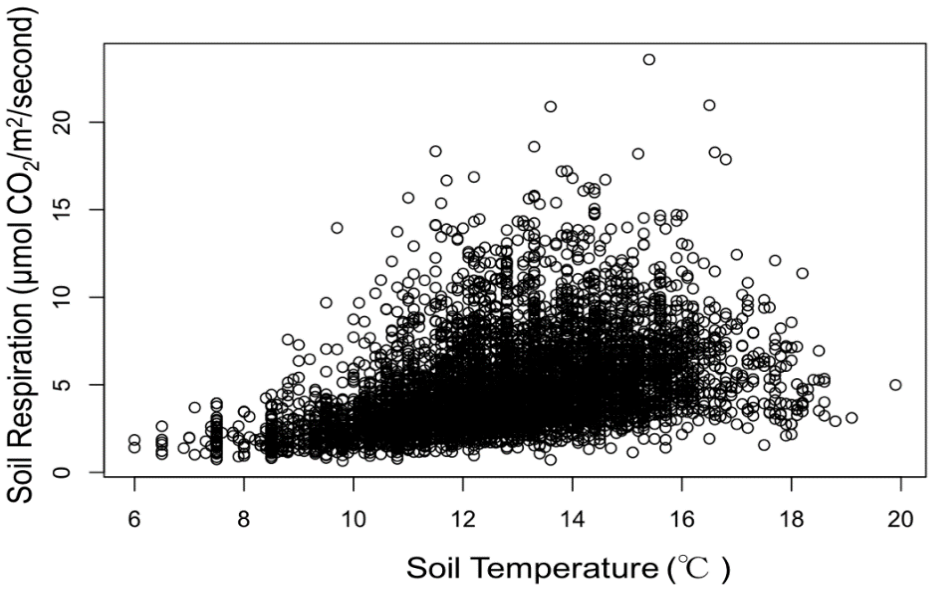

Figure 3. Soil respiration and soil temperatures at 10 cm depth in 13 northern hardwood stands in central New Hampshire across four years (2013, 2014, 2016, 2017).

In addition, I conducted an analysis of differences among plots for each individual stand using TSR data of 2014, 2016, and 2017 (two more respiration collars were added to each plot after 2013). Note that these statistical models at the stand level allow evaluation of differences in response among plots but not a rigorous test of the fertilization effects since treatments were not replicated within stands. As shown in Figure 4, adding N consistently lowered TSR in all three young stands. A similar trend was observed across four out of five old stands as well (the exception being JBO). On the contrary, adding P appeared to lower TSR in four stands at BEF (C1, C3, C5 and C7), whereas P addition stimulated respiration in two old stands (C9 and HBO). Adding N + P tended to lower TSR in seven of the thirteen stands, including some of each age class (C2, C3, C5, C6, JBM, C8, and JBO). Compared to young and old stands, mid-aged stands seemed relatively insensitive to nutrient additions, except the apparent reduced respiration by N+P addition in three of the five mid-age stands. These variable responses indicate that stand or site conditions influence the response of TSR to nutrient addition in northern hardwood forests.

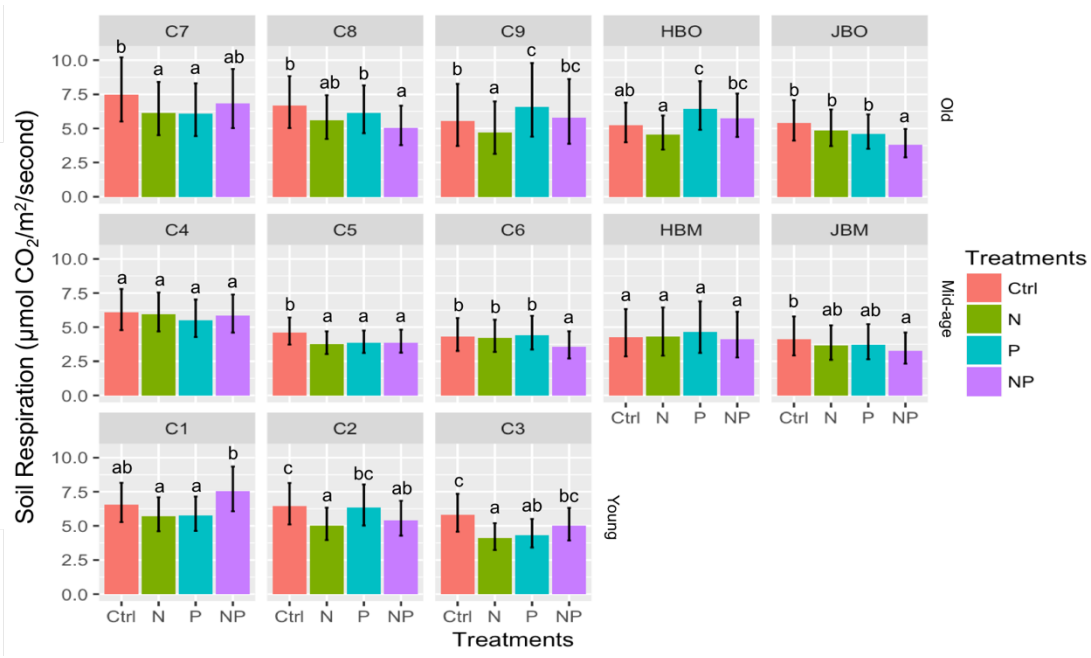

Figure 4. The mean soil respiration rates of three years (2014, 2016, 2017) by stand, age and treatment; bars with different letters for each individual stand are significantly different ($p < 0.05$). Top to bottom panels: old stands, mid-age stands, and young stands.

To assess the relationship between the soil respiration response to nutrient additions and site fertility, I plotted the overall mean response ratios ([fertilized – control]/control) in 2014, 2016, and 2017 against four pre-treatment, stand-level soil fertility indexes (nitrification, N mineralization, bicarbonate extraction of P, and resin extraction of P) (Kang et al., 2016). The coefficient of determination values of 24 separate analyses ranged from 0.000 to 0.261 and were not statistically significant. I did not observe the positive correlation between TSR response ratio and N mineralization in the mineral soil that was reported for the second and third year of fertilization (2012 - 2013) by Kang et al. (2016). Similarly, I plotted TSR response ratios for 2014 measurements against microbial respiration as estimated using lab incubations of soils from all the plots in 2014 (M. Fisk, unpublished data). Again, no

significant correlation was observed (Figure 5). Thus, differences in the response of TSR to nutrient additions could not be explained either by pre-treatment site fertility or by heterotrophic respiration potential.

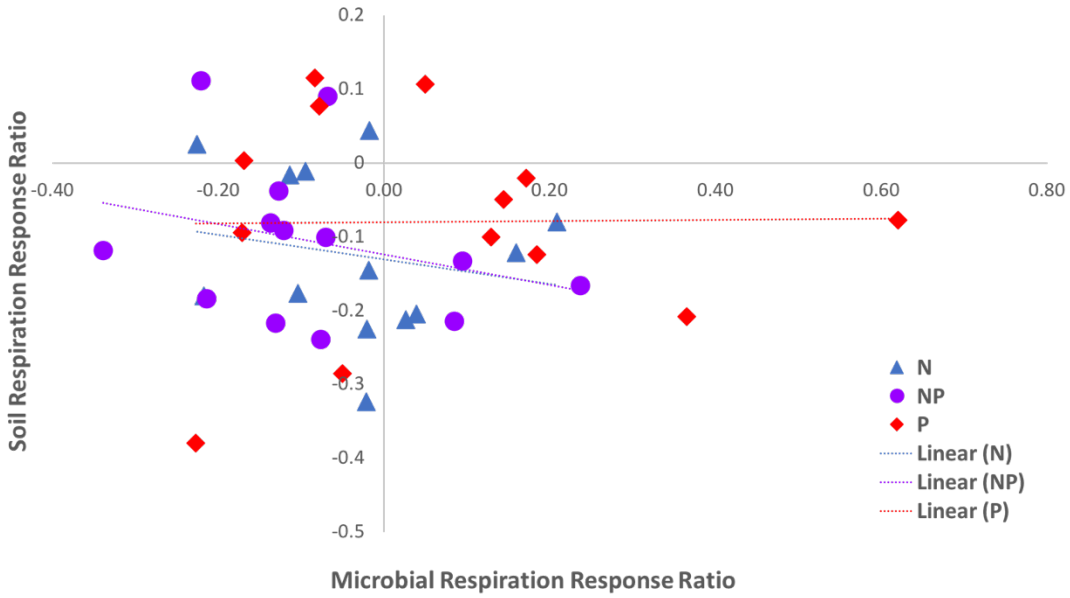

Figure 5. 2014 soil respiration response ratio ((fertilized-control)/control) plotted against 2014 microbial respiration response ratio (R^2 ranges 0.0002 – 0.0804).

4. Discussion

My overall observation of the effects of low-level nutrient addition from 2011 to 2017 on TSR of northern hardwood forests supported my hypothesis that nitrogen enrichment would result in lower TSR rates, especially in young forest stands that appear to be more N limited (Goswami et al., 2018). However, adding P or adding N + P led to conflicting results across different stands. Moreover, I was able to detect significant N x P and the N x P x Age interactions, adding more complexity to the whole picture. Perhaps it should not be surprising that complex responses were observed; it seems likely that some of the variable effects of the treatments reflected interacting or counteracting effects of N vs P on the various processes that contribute to TSR. Moreover, Kang et al. (2016) reported that responses of TSR to nutrient addition in these stands developed gradually, with no effects observed in the first year of treatment. My study showed evidence that more effects, especially complex interactions, can develop after five to six years of low-level fertilization.

Effects of nitrogen on forest TSR have often been reported. There is convincing evidence that adding nitrogen, through either fertilization or atmospheric nitrogen deposition, can lower forest TSR (Janssens et al., 2010; Zhou et al., 2014). The suppression effect could have worked on the autotrophic or the heterotrophic component, or both, involving several possible mechanisms, including C allocation to roots and mycorrhizal fungi (Phillips and Fahey, 2007; Bae et al., 2015), and changes in heterotrophic activity in litter decomposition and soil organic matter processing (Hobbie, 2008).

Particularly, studies attribute lowered heterotrophic respiration rates following inorganic N addition to various competing mechanisms. Studies suggest compositional shifts of saprotrophic communities lead to changes in decomposition rates (Gallo et al., 2004; Zhou et al., 2014; Leff et al., 2015). For example, Allison et al. (2007) observed decreased Basidiomycete diversity in litter and total fungal diversity in soil and changes in community structure in boreal ecosystems under N addition. While there is debate over how the microbial community and function changes in response to N amendment, several studies suggest that adding inorganic N inhibits synthesis and activity of ligninolytic enzymes by white rot fungi (Waldrop and Zak, 2006) and possibly other groups of microbial decomposers (Gallo et al., 2004). Indeed, several studies reported lignin-degrading enzymes, such as phenol oxidases and peroxidases, are down-regulated by N addition (Saiya-Cork et al., 2002; Gallo et al., 2004; Jian et al., 2016). However, conflicting evidence argued that adding N had no effect on lignin degrading enzyme activity, but reduced microbial biomass thereby causing the decreased decomposition and heterotrophic respiration (Keeler et al., 2009; Riggs and Hobbie, 2016). There is general agreement in literature that microbial biomass declines in response to N fertilization (Treseder, 2008). Moreover, abiotic chemical and physical reactions of N fertilizer and soil organic matter can produce compounds that are highly resistant to microbial degradation (Hobbie, 2000; Jassens et al., 2010); such stabilization processes might also play a role in the reduced decomposition and TSR.

The aforementioned mechanism(s) could have contributed to reduced CO_2 efflux in our N and N + P treated plots as observed in the young and old stands. Lab incubation of the Oe and Oa horizons from our plots in 2014 suggested slight suppression of microbial respiration (ca. 10%) in N addition treatments but no effect on microbial biomass C (Fisk et al., 2014). A follow-up study (Shan et al., in press) shows that rhizosphere microbial properties in our young stands are mainly responsive to N availability, but that N effects differ significantly between tree species (red maple vs. yellow birch). Such complex responses could contribute to the variation in responses of TSR across stands with different ages and species compositions. However, the insignificant correlation between 2014 microbial respiration potential response ratios and 2014 or 2014-2017 TSR response ratios indicate that we cannot conclusively attribute the changes in TSR responses to microbial respiration. Conducting the same analysis with more recent microbial respiration data could help account for the possible influence of progressive changes in microbial activity on responses of TSR.

Alternatively, differences in the response of TSR to nutrient additions among the stands might be attributed to root respiration. Fahey et al. (2005) estimated that root respiration comprised about 60% of total TSR in mature northern hardwood forests at Hubbard Brook, NH; thus, changes in this flux could certainly contribute significantly to the TSR response. Root respiration flux could vary with either or both root biomass or specific root respiration rate among treatments. My ongoing work is evaluating the response of fine root biomass in these thirteen stands, and this information should help to inform the causes of the complex patterns of TSR response that I reported here.

In sum, my study shows that the responses of TSR rates in northern hardwood forests depend on forest age as well as the nutrients applied (N, or P, or N+P). Interactions between N and P and age classes did influence soil carbon efflux, but these effects were not consistent across study stands, and were not clearly linked with pretreatment site fertility or microbial respiration response ratios averaged across the three soil horizons (Oe, Oa, and B). The high variation in TSR response to nutrient additions observed across this suite of northern hardwood stands calls into question the notion that forest C fluxes can be predicted with simple functional responses as employed in large-scale models of land-air-ocean interactions.

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